

Emended Neodactylariales (Dothideomycetes): *Szaferohypha* gen. nov. and phylogenetically related genera

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Abstract

Epiphytic fungi evolved several times in Dothideomycetes, particularly within the orders Asterinales, Capnodiales, Microthyriales, and Zeloasporiales, but also in other, less obvious lineages. In this study, a new genus and species, *Szaferohypha* and *S. enigmatica*, isolated from the sooty mould community on the leaves of *Symphoricarpos albus* in Poland, are described based on morphology and phylogenetic analysis using sequences of four DNA loci (LSU, ITS, SSU, and *rpb2*). Due to single isolation, it is unclear whether *Szaferohypha enigmatica* represents a very rare or accidental inhabitant of sooty mould communities. *Szaferohypha* is assigned to the poorly known family Neodactylariaceae and order Neodactylariales, together with *Beaucarneomyces*, *Neodactylaria*, and *Pseudoarthrographis*. The order and family were originally circumscribed based on the features of the genus *Neodactylaria*. Therefore, they are emended by characters of *Beaucarneomyces*, *Pseudoarthrographis*, and *Szaferohypha*.

Key words: Ascomycota, emended descriptions, one new genus, one new species, sooty mould communities, taxonomy



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Introduction

The class Dothideomycetes is megadiverse and the largest class of fungi in the phylum Ascomycota (Wijayawardene et al. 2014, 2020). Currently, the class is divided into 54 orders and 226 families and contains about 20,000 described species (Abdollahzadeh et al. 2020; Hongsanan et al. 2020a, 2020b; Barreto et al. 2024; Pem et al. 2024; Piątek et al. 2024). The best-known and studied orders are Capnodiales s. lato, Dothideales, Botryosphaeriales, and Pleosporales (Zhang et al. 2012; Phillips et al. 2013, 2019; Quaedvlieg et al. 2014; Thambugala et al. 2014; Yang et al. 2017; Videira et al. 2017; Abdollahzadeh et al. 2020). Other orders of Dothideomycetes are less known, primarily because their members are less common in the environment, although some of them are important for human life and the economy (Hongsanan et al. 2020b; Shen et al. 2020).

The high species diversity observed in Dothideomycetes is reflected by the wide geographical range and diversity of lifestyles of its members. They are known from all areas of the world and habitats, even capable of colonizing extreme habitats such as cold deserts (Coleine et al. 2020), deep-sea sediments,

including methane sediments (Nagahama et al. 2011; Rojas-Jimenez et al. 2020), saline waters (Czachura et al. 2021), acidic environments (Kolařík et al. 2021), and resin exudates (Czachura and Janik 2024). Species of Dothideomycetes are plant pathogens, saprobes, rock-inhabiting fungi, lichens, endophytes, and epiphytes. Hongsanan et al. (2016) defined fungal epiphytes as species occurring on the living plant surfaces, especially leaves, which belong to the following orders of Dothideomycetes: Asterinales, Capnodiales, Microthyriales, Zeloasperisporiales, and Meliolales in Sordariomycetes. However, epiphytes are also known in other, less obvious lineages (Piątek et al. 2023, 2024). The special kind of epiphytes are sooty moulds, which live on leaves/needles covered with exudates of phloem-feeding insects, especially honeydew secreted by aphids (Hughes 1976).

Recently, we isolated an enigmatic fungus from a sooty mould colony on *Symphoricarpos albus* in southern Poland, which showed affinities to members of the poorly known order Neodactylariales (Qiao et al. 2020; Crous et al. 2024). In this study, a novel species accommodated in a new genus is described for this fungus. The phylogenetic placement of this new genus and its most closely related genera are analysed, and emended descriptions of the order Neodactylariales and family Neodactylariaceae are provided.

Materials and methods

Strains and morphological analyses

The strain was isolated from the sooty mould community on *Symphoricarpos albus* leaves planted in municipal greenery in southern Poland (see Piątek et al. 2023). Macroscopic features of cultures were observed and photographed using 4-week-old colonies grown on MEA and PDA at 6 °C, 15 °C, and 25 °C, as well as 15-week-old colonies grown on MEA and PDA at 15 °C. Description of culture characteristics is based on 4-week-old colonies. The morphology of colonies observed after 15 weeks is briefly mentioned in the subsection “notes”. Growth at different temperatures was assessed by measuring the colony diameter after 4 weeks. Microscopic features were analysed using colonies older than 8 weeks grown on MEA at 15 °C. Hyphae and conidia taken from the edge of the colony were mounted in lactic acid (80%) on microscope slides and examined under a Nikon Eclipse 80i light microscope. Microscopic structures were measured and photographed using NIS-Elements BR 3.0 imaging software. The holotype is a dried specimen obtained from culture and deposited in the fungal collection of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (KRAM F). Culture is preserved in the culture collection of the Westerdijk Fungal Biodiversity Institute (CBS) and in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. The morphological characteristics of *Beaucarneamyces* and *Pseudoarthrographis* used for the emendation of Neodactylariales and Neodactylariaceae are taken from the literature (Crous et al. 2018, 2024).

DNA isolation, PCR, and sequencing

After growth of cultures for about one month, genomic DNA was extracted from a portion of mycelium using the DNeasy® Plant Mini Kit (Qiagen, Germany). To conduct molecular studies, four genetic loci were amplified, namely ITS1-5.8S-

ITS2 rDNA (= ITS), 28S D1–D2 rDNA (= LSU), a small subunit rDNA (= SSU), and a protein-coding gene—a partial DNA-directed RNA polymerase II second largest subunit (*rpb2*). To amplify the loci mentioned above, four different primer pairs were used: ITS1 and LR5 for a fragment containing ITS and LSU (White et al. 1990; Vilgalys and Hester 1990), NS1 and NS4 for SSU (White et al. 1990), and fRPB2-5F and fRPB2-7cR for *rpb2* (Liu et al. 1999). Polymerase chain reactions (PCR) for all loci were performed in a reaction mixture prepared as described in Piątek et al. (2023). Amplification conditions for PCR reactions of the fragment containing ITS and LSU were performed as described by Piątek et al. (2023); in turn, amplification conditions for SSU and *rpb2* were described by Piątek et al. (2024). The PCR products were checked on 1% agarose gels and enzymatically purified using Exo-BAP Mix (EURx, Gdańsk, Poland). DNA sequencing was carried out in both directions by MacroGen Europe B.V. (Amsterdam, the Netherlands). ITS was sequenced using primers ITS1 and ITS4; LSU was sequenced using primers LSU1Fd and LR5; and SSU and *rpb2* were sequenced with the same pairs of primers that were used for amplification.

Phylogenetic analysis

The affinities of obtained ITS, LSU, SSU, and *rpb2* sequences of the isolated fungus were performed in the NCBI's GenBank nucleotide database using the megablast search tool (Zhang et al. 2000). To resolve its phylogenetic position, the multilocus dataset containing LSU, ITS, SSU, and *rpb2* sequences of representatives of Dothideomycetes used by Maharachchikumbura et al. (2021, with some modifications) was obtained. The dataset was, among others, augmented by sequences of representatives of the orders Neodactylariales (*Beaucarneya*, *Neodactylaria*, *Pseudoarthrographis*) and Oncopodiellales (*Diplocydiella*, *Oncopodiella*) (Suppl. material 1). Sequences were separately aligned for each single-gene dataset using the MAFFT algorithm (Katoh et al. 2005) in Geneious 11.1.5 and concatenated. Phylogenetic relationships were inferred using the concatenated LSU-ITS-SSU-*rpb2* alignment by the maximum likelihood (ML) analysis using RAxML-NG v. 1.1.1 (Kozlov et al. 2019), with 1000 bootstrap replicates. The best-fit substitution models were selected with ModelTest-NG v. 0.2.0 using the Bayesian Information Criterion (BIC) (Darriba et al. 2020). The final phylogenetic tree was visualized using FigTree v1.4.3. The alignment was deposited at figshare.com (<https://doi.org/10.6084/m9.figshare.27231756.v1>).

Results

Phylogenetic analysis

The concatenated multilocus dataset (LSU, ITS, SSU, and *rpb2*) included sequences of 154 representatives of most of the orders of the class Dothideomycetes, including all representatives of Neodactylariales, and a member of the class Arthoniomycetes (*Schismatomma decolorans*) used as an outgroup. The concatenated alignment contained 4483 characters (LSU: 1082, ITS: 750, SSU: 1761, *rpb2*: 890, including alignment gaps). The best-fit substitution models selected for single-gene alignments were as follows: GTR+I+G4 for both ITS and LSU, TrNef+I+G4 for SSU, and TPM3uf+I+G4, TPM2uf+I+G4, and TIM2+I+G4

for *rpb2* (three codons). The phylogenetic tree resulting from maximum likelihood analysis is shown in Fig. 1. Representatives of Dothideomycetes formed lineages that correspond to the orders that were well supported, but relationships between orders were mostly not resolved. The strain of a new genus and species, *Szaferohypha enigmatica*, clustered within the lineage assigned to the order Neodactylariales, but its relationship to the remaining genera of this order (*Beaucarneamyces*, *Neodactylaria*, and *Pseudoarthrographis*) was not resolved. The clustering of genera assigned to Neodactylariales was well supported (MLB = 85%), and this order formed a strongly supported (MLB = 98%) sister group to the lineage assigned to the order Oncopodiellales that was fully supported (MLB = 100%).

Taxonomy

Neodactylariales H. Zheng & Z.F. Yu, MycoKeys 73: 74 (2020), emend. Piątek, Stryjak-Bogacka & Czachura

Description. Asexual morph from human-associated organs or saprobic on plant debris **or epiphytic on living leaves**. Conidiophores acroauxic, macronematous **or micronematous**, mononematous, branched or unbranched, **or reduced to conidiogenous cells**. Conidiogenous cells mono- and polyblastic, sympodially extended **or not**. Conidia solitary **or in branched or unbranched chains**, hyaline or pale pigmented, smooth, verrucous, or echinulate. **Chlamydospores sometimes present**. Sexual morph not observed.

Type genus. *Neodactylaria* Guevara-Suarez, Deanna A. Sutton, Wiederh. & Gené.

Notes. Because of the inclusion of genera *Beaucarneamyces*, *Pseudoarthrographis*, and *Szaferohypha* in Neodactylariales (Crous et al. 2024; this study), the emended description of this order is necessary. The original description of this order (Qiao et al. 2020) is included without changes and emended by crucial characters of these genera given in bold.

Neodactylariaceae H. Zheng & Z.F. Yu, MycoKeys 73: 75 (2020), emend. Piątek, Stryjak-Bogacka & Czachura

Description. Mycelium superficial or immersed, composed of branched, septate, hyaline to subhyaline hyphae. Conidiophores macronematous **or micronematous**, mononematous, straight or flexuous, septate, unbranched, **or reduced to conidiogenous cells**. Conidiogenous cells terminal or intercalary, **monoblastic or polyblastic**, sympodial **or not**, with short-cylindrical denticles **or without denticles**. Conidial secession schizolytic. Conidia solitary **or in branched or unbranched chains**, smooth or finely echinulate. **Chlamydospores sometimes present**. Sexual morph not observed.

Type genus. *Neodactylaria* Guevara-Suarez, Deanna A. Sutton, Wiederh. & Gené.

Notes. The order Neodactylariales contains one family, Neodactylariaceae, that is emended by features of genera *Beaucarneamyces*, *Pseudoarthrographis*, and *Szaferohypha*. The original description of this family (Qiao et al. 2020) is included without changes, and the emended part is given in bold.

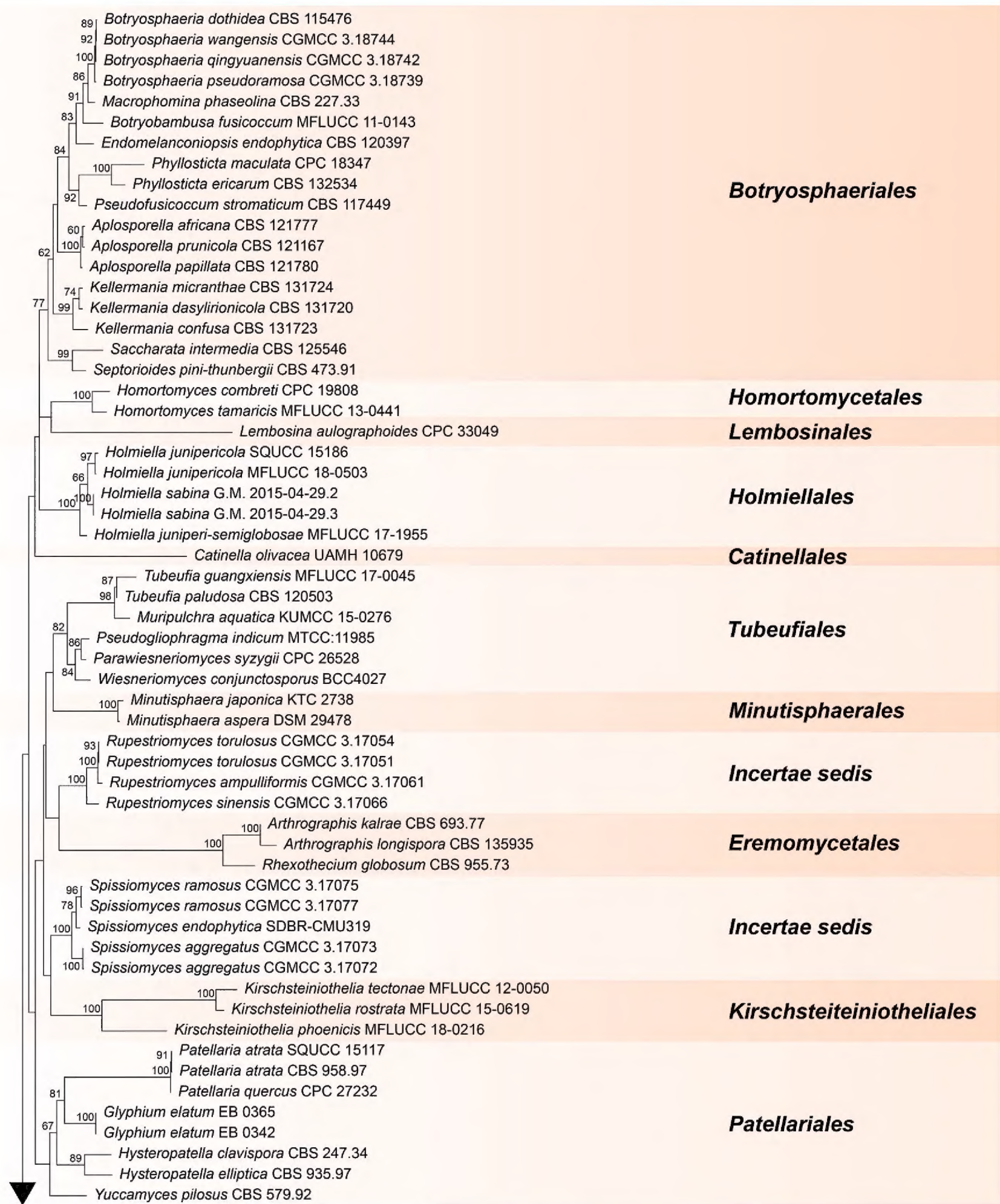


Figure 1. Phylogenetic tree of selected representatives of the orders of Dothideomycetes, including all sequenced species of Neodactylariales, obtained from a maximum likelihood analysis of the combined multi-locus alignment (LSU, ITS, SSU, *rpb2*). The position of *Szaferohypha enigmatica* is indicated in bold. Numbers above branches indicate maximum likelihood bootstrap (MLB) support values > 50%. *Schismatomma decolorans* AFTOL-ID 307 was used as an outgroup. The scale bar represents the expected number of changes per site.

***Szaferohypha* Piątek, Stryjak-Bogacka & Czachura, gen. nov.**

MycoBank No: 856722

Etymology. Named after Polish botanist and palaeobotanist Professor Władysław Szafer (1886–1970), the first director of the W. Szafer Institute of Botany, Polish Academy of Sciences.

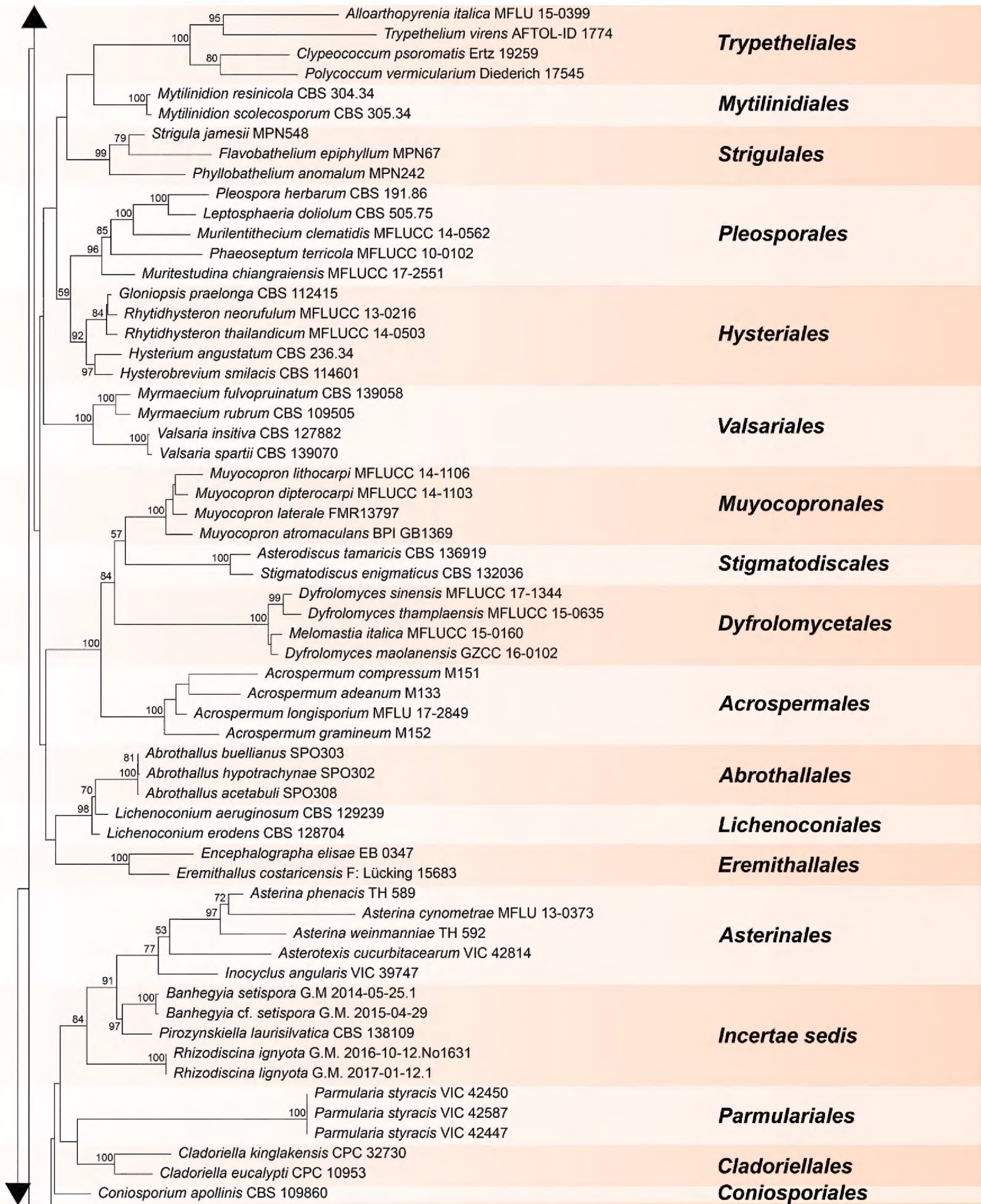


Figure 1. Continued.

Description. Colonies erumpent, spreading, umbonate, grayish-brown, with a velvety surface caused by abundant aerial mycelium, margin undulate. Mycelium composed of branched, septate, hyaline, subhyaline, pale brown, or brown, smooth or verrucose, usually thick-walled hyphae. Conidiophores micronematous, reduced to conidiogenous cells, rarely macronematous. Conidiogenous cells terminal, rarely lateral, monoblastic, hyaline, subhyaline, pale brown, or brown. Conidia globose, subglobose, rarely broadly ellipsoid, hyaline, subhyaline, or brown, aseptate, rarely with 1–2 septa or muriformly septate, smooth or finely verrucose, thick-walled, sometimes produced intercalary.

Type species. *Szaferohypha enigmatica* Piątek, Stryjak-Bogacka & Czachura.

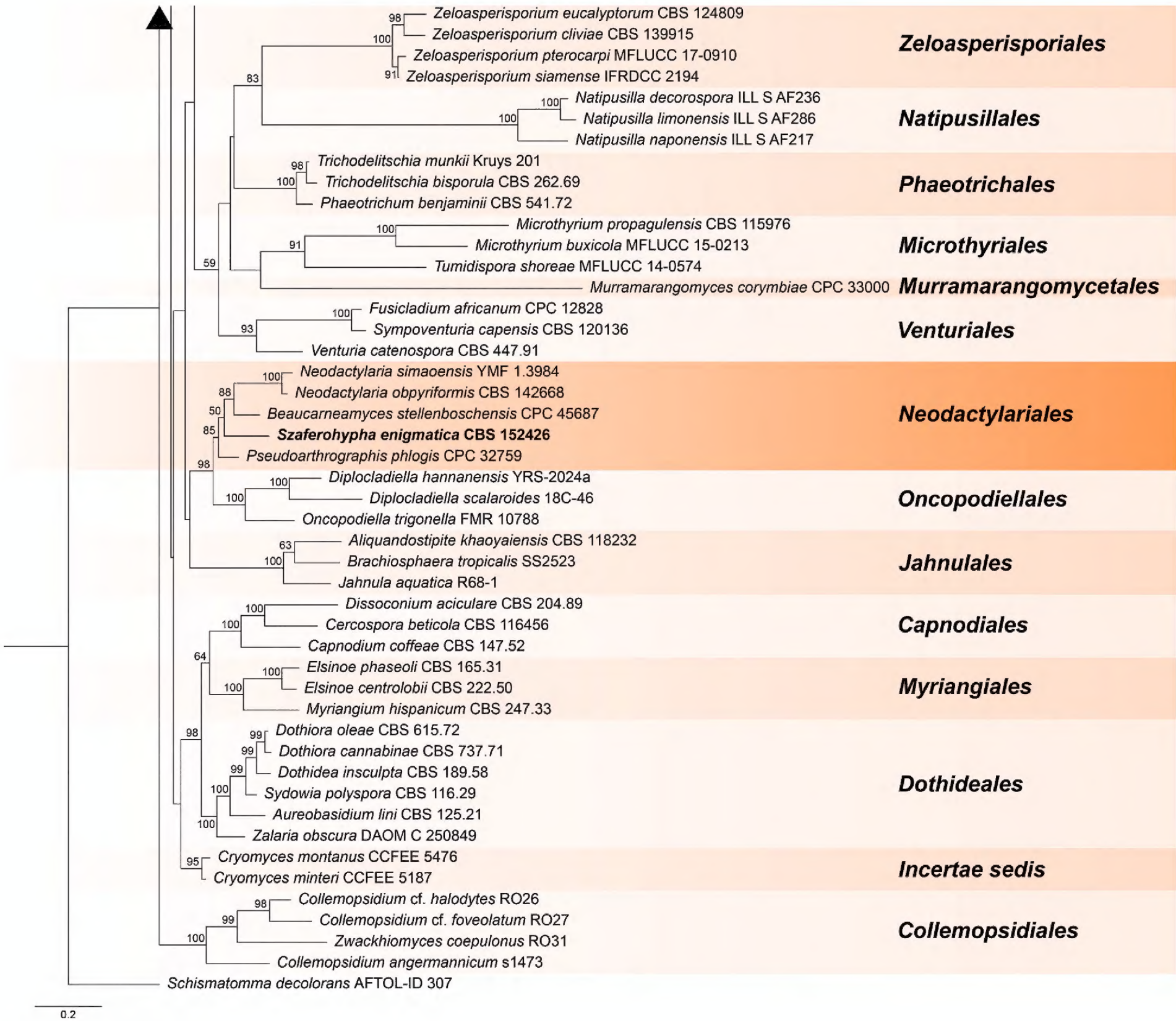


Figure 1. Continued.

***Szaferohypha enigmatica* Piątek, Stryjak-Bogacka & Czachura, sp. nov.**

MycoBank No: 856723

Figs 2–4

Etymology. Refers to the uncertain taxonomic position of this fungus after the first molecular analyses.

DNA barcodes. ITS (PQ479987), LSU (PQ479989), SSU (PQ479988), *rpb2* (PQ475069).

Typus. POLAND • Małopolska Province, Tarnów County: Tarnów–Piaskówka, municipal greenery, isolated from sooty mould community on *Symphoricarpos albus* leaves, 1 Oct. 2018, leg. M. Piątek, W. Bartoszek & P. Czachura (holotype KRAM F-59996; culture ex-type: G191 = CBS 152426).

Description. Mycelium composed of branched, septate, hyaline, subhyaline, pale brown, or brown, smooth or verrucose, usually thick-walled hyphae, 2–4 µm, sometimes with oil guttules; wall ca. 0.5 µm thick. Conidiophores micronematous, reduced to conidiogenous cells, rarely macronematous. Conidiogeneous cells terminal, rarely lateral, monoblastic, hyaline, subhyaline, pale brown, or

brown, $3.5\text{--}13.5 \times 2.5\text{--}4.5 \mu\text{m}$. Conidia globose, subglobose, rarely broadly ellipsoid, hyaline, subhyaline, or brown, aseptate, rarely with 1–2 septa or muriformly septate, smooth or finely verrucose, thick-walled, $6.5\text{--}15 \times 6\text{--}13.5 \mu\text{m}$, sometimes germinating into hypha or produced intercalary, wall ca. $0.5\text{--}1.5 \mu\text{m}$ thick.

Culture characteristics. Colonies on MEA erumpent, spreading, umbonate, grayish, reaching 1 mm diam. after 4 weeks at 6 °C, 4 mm diam. after 4 weeks at 15 °C, and 8 mm diam. after 4 weeks at 25 °C, with a velvety surface caused by abundant aerial mycelium, margin entire. Reverse black. Colonies on PDA erumpent, spreading, umbonate, grayish-brown, reaching 3 mm diam. after 4 weeks at 6 °C, 4 mm diam. after 4 weeks at 15 °C, and 7 mm diam. after 4 weeks at 25 °C, with a velvety surface caused by abundant aerial mycelium, margin finely undulate. Reverse black.

Notes. Colonies photographed after 15 weeks of growth, depicted in Fig. 2g, h, are radially folded on MEA or folded on PDA, possess abundant aerial mycelium, grayish with white patches on MEA and brown with grayish patches on PDA, and are distinctly undulate at the margin.

Based on a megablast search of NCBI's GenBank nucleotide database, the closest hits of the named species using the ITS sequence are *Pseudoarthrographis phlogis* (strain CPC 32759, GenBank MH327796; identities = 370/414 (89%), 11 gaps (2%)), *Oncopodiella trigonella* (strain FMR 10788, GenBank KY853455; identities = 356/408 (87%), 11 gaps (2%)), and *Xylographa parallela* (voucher Z. Palice 22099 (PRM), GenBank MK778618; identities = 344/396 (87%), seven gaps (1%)). The closest hits of the named species using the LSU sequence are *Beauvernia mycelium* (strain CPC 45687, GenBank PP791445; identities = 826/873 (95%), four gaps (0%)), *Pseudoarthrographis phlogis* (strain CPC 32759, GenBank NG_064540; identities = 835/883 (95%), no gaps), and *Umbilicaria hypococcinea* (strain A12, GenBank JQ739991; identities = 876/927 (94%), eight gaps (1%)). The closest hits using the SSU sequence are *Cophinforma atrovirens* (strain CSM_72, GenBank MF436134; identities = 857/870 (99%), no gaps), *Gloeopycnis protuberans* (specimen DAOM 745762, GenBank NG_067652; identities = 857/870 (99%), no gaps), and *Botryosphaeria mamane* (strain CBS 117444, GenBank KF531821; identities = 857/870 (99%), no gaps). The closest hits using the *rpb2* sequence are *Shiraia bambusicola* (voucher SICAUCC 23-0005, GenBank OR424351; identities = 237/283 (84%), six gaps (2%)), *Lindra obtusa* (strain AF-TOL-ID 5012, GenBank FJ238382; identities = 207/252 (82%), three gaps (1%)), and *Natonodosa speciosa* (strain CLM-RV86, GenBank MH745150; identities = 217/266 (82%), six gaps (2%)). In the case of SSU and *rpb2*, the sequences of these two regions are not available for representatives of the most closely related genera, namely *Beauvernia* and *Pseudoarthrographis*.

Discussion

In this study, morphological and phylogenetic analyses were conducted to identify the enigmatic fungal strain isolated from sooty mould biofilm on the surface of *Symphoricarpos albus* leaves. In consequence, the isolated fungus is described as a new genus and species, *Szaferohypha enigmatica*, and assigned to the order Neodactylariales. Three genera were previously included in this order, namely *Beauvernia*, *Neodactylaria*, and *Pseudoarthrographis* (Qiao et al. 2020; Crous et al. 2024), and *Szaferohypha* is morphologically different from all of them.

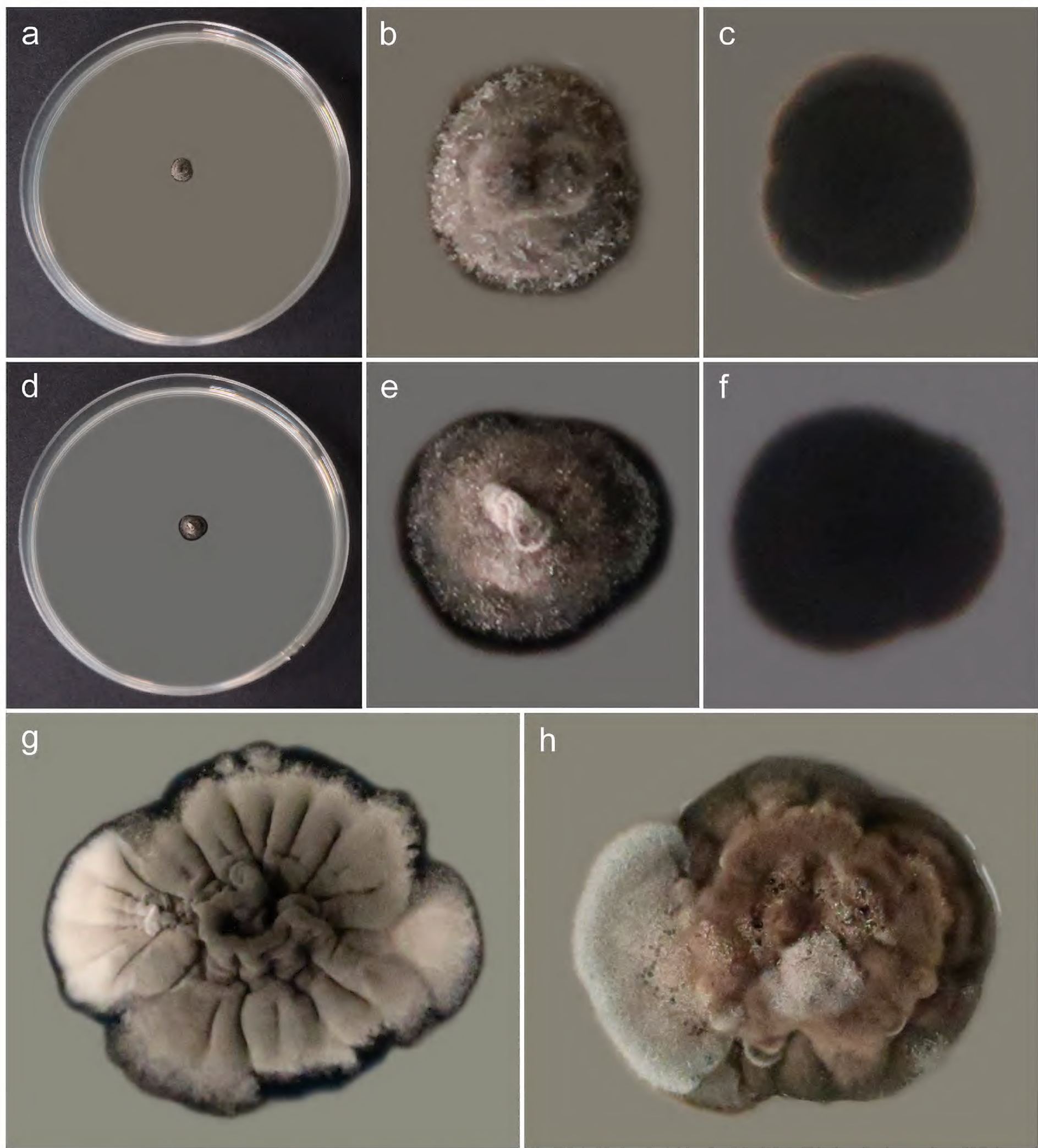


Figure 2. Morphology of cultures of *Szaferohypha enigmatica* (strain G191 = CBS 152426) after 4 weeks of growth at 25 °C **a–c** general view, upper side and reverse side of colony on MEA **d–f** general view, upper side and reverse side of colony on PDA **g** general view of 15-week-old colony on MEA (to show difference in morphology) **h** general view of 15-week-old colony on PDA (to show difference in morphology).

Beaucarneamyces, with type species *B. stellenboschensis*, was described from dead leaves of *Beaucarnea stricta* in South Africa and is characterized by hyaline conidiophores reduced to conidiogenous cells that are polyblastic with several apical denticles. Conidia in this genus are solitary, fusoid-ellipsoid, hooked, 3-septate, hyaline but with pale brown central cells (Crous et al. 2024). *Neodactylaria* is typified with *N. obpyriformis* described from human bronchoalveolar lavage in the USA (Crous et al. 2017). The second species in

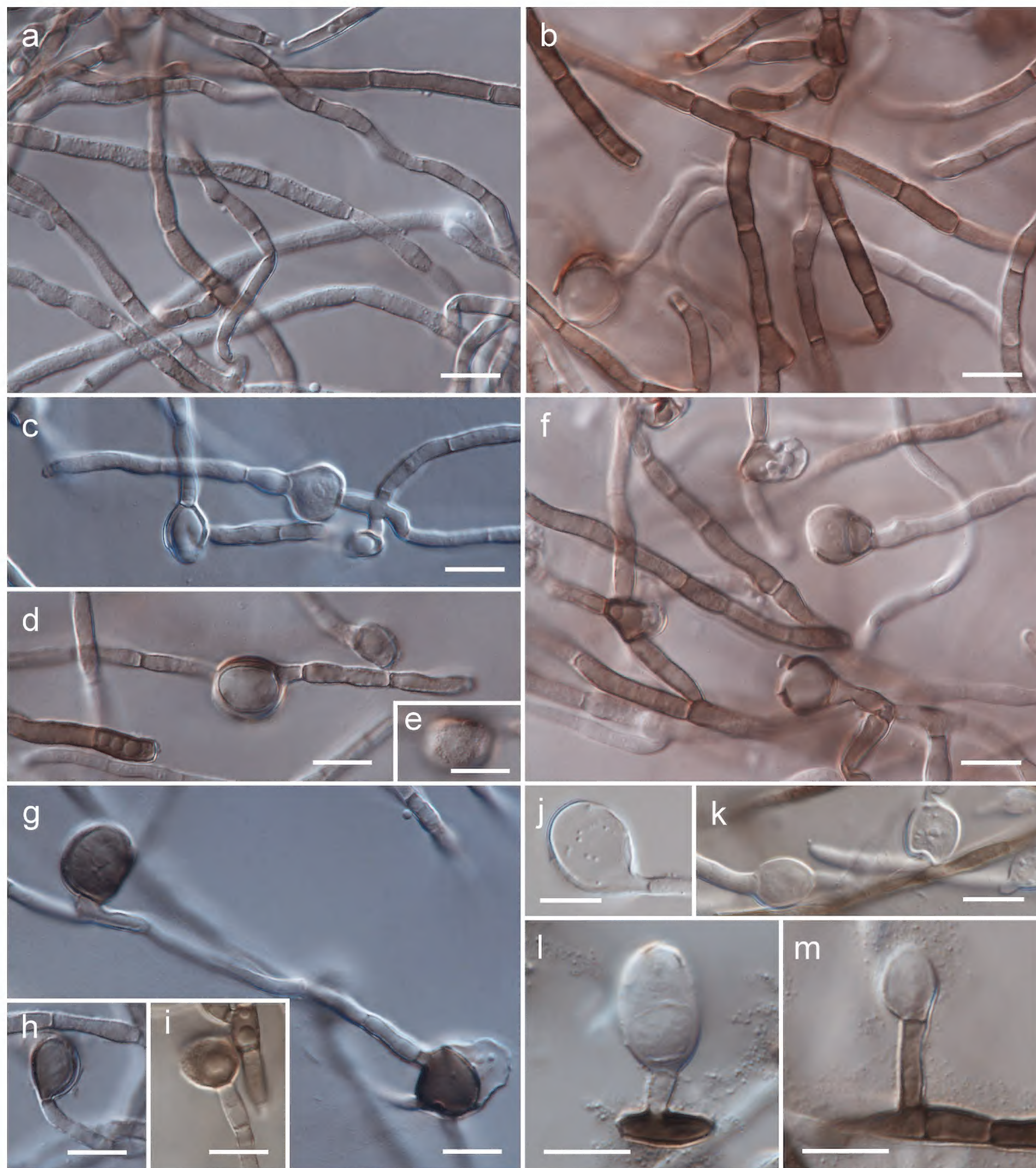


Figure 3. Morphology of *Szaferohypha enigmatica* (strain G191 = CBS 152426, all on MEA) **a, b** subhyaline or brown, smooth or verrucose hyphae **c–e** subhyaline or brown intercalary conidia (figure **e** depicts the verrucose surface of the conidium) **f** hyphae and terminal conidia **g–m** hyaline or brown, lateral or terminal conidia emerging on conidiogenous cells (figure **i** depicts the verrucose surface of the conidium). Scale bars: 10 µm.

this genus is *N. simaoensis*, described from submerged unidentified dicotyledonous leaves in China (Qiao et al. 2020). *Neodactylaria* is characterized by having straight or flexuous, brown conidiophores with polyblastic, sympodial, and denticle-like conidiogenous loci, which form solitary, obpyriform or rostrate, 0-1-septate, pale brown conidia (Crous et al. 2017). *Pseudoarthrographis*, with a type species *Pseudoarthrographis phlogis* described from *Phlox subulata*



Figure 4. Morphology of *Szaferohypha enigmatica* (strain G191 = CBS 152426, all on MEA) **a, b** terminal conidia emerging on conidiogenous cells **c** detached conidium. Scale bars: 10 µm.

in New Zealand, has smooth hyphae and smooth, 0–1-septate cylindrical arthroconidia with truncate ends produced in branched or unbranched chains. In culture it also forms smooth, globose chlamydospores occurring in chains (Crous et al. 2018).

Despite numerous strains obtained during our studies of sooty mould communities, only a single strain belonging to *Szaferohypha enigmatica* was isolated. It is therefore unclear whether this species represents a very rare or accidental inhabitant of these communities and its main habitat is elsewhere.

The order Neodactylariales, with one family Neodactylariaceae, was originally described to accommodate only one genus, *Neodactylaria*, containing two species in China and the USA (Crous et al. 2017; Qiao et al. 2020). Recently, two monotypic genera, *Beaucarneomyces* and *Pseudoarthrographis*, containing species known in South Africa and New Zealand, respectively, were assigned to this order by Crous et al. (2024). Here, yet another monotypic genus, *Szaferohypha*, known from Poland, is added to Neodactylariales. Thus, currently this order includes fungi living in opposite corners of the world. The order Neodactylariales and family Neodactylariaceae were originally circumscribed based on characters known in the genus *Neodactylaria* (Qiao et al. 2020). They therefore need emendation by the features of the genera *Beaucarneomyces*, *Pseudoarthrographis*, and *Szaferohypha*. In our phylogenetic analysis, Neodactylariales is related to the order Oncopodiellales that is going to be described (Sun et al. 2024, preprint). Two genera, *Diplocladiella* and *Oncopodiella* (Hernández-Restrepo et al. 2017; Sun et al. 2024, preprint), assigned to two families, Diplocladiellaceae and Oncopodiellaceae, are included in this order (Sun et al. 2024, preprint). The relationships of Neodactylariales and Oncopodiellales are revealed here for the first time.

Sooty mould communities are an underexplored source of rare and undescribed species, of which many are probably extremophilic since they live in extreme environments (Chomnunti et al. 2014). They were previously studied using classical morphological methods (Hughes 1976) that are, however, inadequate to reveal their true diversity, and only recently started to study in modern ways using morphological and molecular methods, though mainly in tropics (Chomnunti et al. 2012, 2014) and much more rarely in temperate regions (Flessa et al. 2012, 2021). In the course of our ongoing studies of sooty mould communities covering the surface of leaves/needles of ornamental plants in

Poland, i.e., in the temperate climate, about 190 species were isolated from these communities (M. Piątek et al. unpublished data), being either as constant or accidental colonizers, of which many are undescribed. These include four new *Rachicladosporium* species (Piątek et al. 2023), a new *Lapidomyces* species (Crous et al. 2023b), a new *Xenoramularia* species (Crous et al. 2023a), a new *Pseudopezicula* species (Crous et al. 2024), and many more that are waiting for description.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

MP: conceptualization, investigation, formal analyses, visualisation, writing—original draft preparation; MSB: investigation, formal analyses, visualisation, writing—review and editing; PC: investigation, visualisation, writing—review and editing. All authors have read and approved the final version of the manuscript.

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Data availability

The data that support the findings of this study are available in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and in culture collections and fungal herbaria, as shown in Suppl. material 1 and the text.

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Supplementary material 1

List of species with strain/specimen and GenBank accession numbers used in phylogenetic analysis

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Data type: docx

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